

LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF  
*PROCECIDOCHARES FLAVIPES* ALDRICH (DIPTERA: TEPHRITIDAE)  
ON *BRICKELLIA* SPP. IN SOUTHERN CALIFORNIA

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*Abstract.*—*Procecidochares flavipes* Aldrich is a multivoltine (at least bivoltine), oligophagous tephritid fly reproducing in flower heads of species of *Brickellia* (Eupatoriaceae: Asteraceae) in California. Unlike all other known species of *Procecidochares*, *P. flavipes* is not an obligate gall former; rather, its larvae feed mainly on the ovules and soft achenes as well as on sap. The egg, third instar larva, and puparium are described and figured; these stages are distinct morphologically from the same stages of other species of *Procecidochares* studied to date in California. Pupariation occurs in the larval feeding chamber inside a bundle of scored achenes. Premating and mating behaviors are described. Newly emerged, sexually immature adults can mate, but then oversummer or overwinter as aestivating adults, probably in riparian habitats, to await flowering by their alternate host plants. *Eurytoma* sp. (Eurytomidae), *Pteromalus* sp. (Pteromalidae), and *Colotrechnus ignotus* Burks (Eupelmidae) are reported as primary parasitoids of *P. flavipes*.

*Key Words:* Insecta, *Procecidochares flavipes*, nonfrugivorous Tephritidae, mating behavior, immature stages, Asteraceae, galls, flower-head feeding

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*Procecidochares flavipes* Aldrich (Diptera: Tephritidae) is the second of 11 described species in this genus from North America north of Mexico (Foote et al. 1993) to be studied by us in California (Green et al. 1993). Preliminary findings on another, still undescribed species from *Ambrosia dumosa* (Gray) Payne were reported by Silverman and Goeden (1980). Herein we report our findings on *P. flavipes*, a species unique for its nongallicolous habit among *Procecidochares* as heretofore known (Foote et al. 1993, Goeden, Headrick, and Teerink, unpublished data).

#### MATERIALS AND METHODS

The principal study area during 1988–1992 was in dense chaparral between 1360- and 1560-m elevations along the unpaved truck trail up Santa Rosa Mountain, San

Bernardino National Forest (southern section), Riverside Co., in southern California. Newly reported, alternate host plants for *P. flavipes* at this location were the spring-blooming host of the F<sub>1</sub> generation, *Brickellia oblongifolia* Nuttall (Asteraceae = Compositae), and the fall-blooming *B. californica* (Torrey and Gray) Gray. One-liter samples of mature flower heads of these and other species of *Brickellia* were collected and returned to the laboratory for dissection, photography, description, and measurement, or for bulk-caging in glass-topped sleeve cages in the insectary of the Department of Entomology, University of California, Riverside at 27 ± 1°C and 14- or 16-h photoperiods (Goeden 1985, 1989). Adults studied either were recovered from these insectary cagings, or were reared along with parasitoids from larvae and puparia

dissected from flower heads and held separately in cotton-stoppered, glass, shell vials within humidity chambers in the laboratory at 22–24°C and 76% R.H. Post-teneral adults were dissected in glycerine mounts for examination of their abdominal organs. The crop was further dissected in 70% EtOH treated with 1% alcoholic acid fuchsin as a visual aid.

Larvae and puparia of *P. flavipes* dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Specimens for SEM later were rehydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH solutions, critical-point dried, mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages fitted with a cotton wick and basal water reservoir and provisioned with honey striped on the lid or also with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cagings were used for longevity studies and oviposition tests. Virgin male and female flies obtained from emergence vials were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton (Headrick and Goeden 1991, Goeden and Headrick 1992) for direct observation, video-recording, and still-photography of their general behavior, courtship, and copulation. Six pairs were held together for at least 1 month, and observations were made as opportunity allowed throughout the day.

Plant names used in this paper follow Munz (1974). Nomenclature used to describe the immature stages follows Headrick and Goeden (1990a, 1991) and Goeden and Headrick (1990, 1991a, b, 1992), and the telegraphic format of Headrick and Goeden

(1993) and Goeden et al. (1993). Means  $\pm$  SE are used throughout this paper. Voucher specimens of reared adults of *P. flavipes* and its parasitoids reside in the research collections of RDG; preserved specimens of larvae and puparia are stored in separate collections of immature Tephritidae maintained by DHH or JAT.

## RESULTS AND DISCUSSION

### Taxonomy

Aldrich (1929) described this species from a female collected on Socorro Island in the Revillagigedo Islands group off the west coast of Mexico. Foote and Blanc (1963) included *P. flavipes* in their key to California species as well as a photograph of a wing of a female. Foote et al. (1993) included *P. flavipes* in their key to North American species as well as a discussion of its recognition features and an annotated wing photograph. Otherwise, the adults have not been illustrated, nor the immature stages heretofore described or illustrated.

Egg.—Egg body smooth, shiny, white, navicular; ova averaged  $0.60 \pm 0.01$  (range, 0.54–0.66) mm long,  $0.18 \pm 0.01$  (range, 0.16–0.20) mm wide ( $n = 16$ ); anterior end bluntly rounded bearing distinct peg-like, 0.02–0.03-mm-long pedicel (Fig. 1).

The egg of *Procecidochares* sp. on *Ambrosia dumosa* is half as long and elongate-ellipsoidal, but bears a similar sized pedicel (Silverman and Goeden 1980). The egg of *P. stonei* is slightly shorter and half as wide as *P. flavipes* (Green et al. 1993), but like *Procecidochares* sp. (Silverman and Goeden 1980), is tapered at both ends.

Third instar larva.—Third instar elongate, elliptical, tapered anteriorly, rounded posteriorly (Fig. 2A); integument white with abdominal dorsum dark brown (Fig. 4C); thoracic segments bear small, unevenly polygonal, rugose pads (Fig. 2E); ventral aspect of intersegmental areas and dorsum of caudal segment bear minute acanthae (Fig. 2A); gnathocephalon conical with elongated ru-

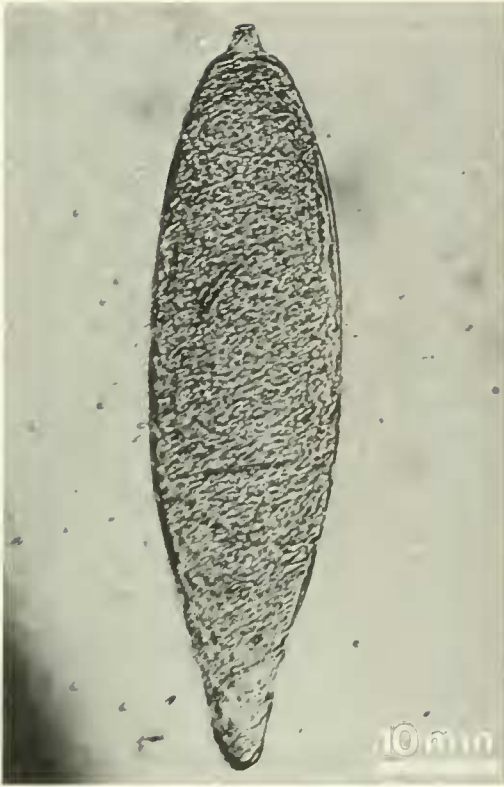


Fig. 1. Egg of *P. flavipes*, pedicel at top (160 $\times$ ).

gose pads near anterior margin, smooth posteriorly (Fig. 2B); paired dorsal sensory organs verruciform (Figs. 2B-1, 2C-1); anterior sensory lobes flattened, separated by a medial depression (Fig. 2B-2) bearing a lateral sensory organ (Fig. 2C-2); pit sensory organ (Fig. 2C-3); terminal sensory organ (Fig. 2C-4); and an additional sensillum dorsad of pit sensory organ (Fig. 2C-5); stomal sense organs lie ventrad of anterior sensory organs near mouth lumen and bear several pit-sensilla (Fig. 2D-1); mouth hooks bidentate, teeth stout, conical (Fig. 2D-2); median oral lobe lanceolate, basally free of labial lobe (Fig. 2D-3); prothorax covered by small, unevenly polygonal rugose pads (Fig. 2E-1); anterior thoracic spiracles dorsolateral on posterior margin of prothorax each bearing two papillae (Fig. 2E-2); lateral and ventral surfaces of mesothorax and metathorax bearing small, rugose pads, dor-

sum bearing minute acanthae; intersegmental areas bearing rows of minute acanthae; lateral spiracular complex found near anterior margins of segments TII–AVII, each composed of a single, open, lateral spiracle (Fig. 2F-1), and a single, verruciform sensillum (Fig. 2F-2); caudal segment bears posterior spiracular plates; plates bear three oval rimae ca. 0.02 mm long (Fig. 2G-1); and four thorn-like interspiracular processes, the longest measuring 0.01 mm (Fig. 2G-2); stelex-type sensilla surround margin of caudal segment in four-dorsal, six-ventral arrangement; additionally, caudal segment bears a pair of compound sensilla ventrad of spiracular plates consisting of two, stelex-type sensilla (Fig. 2H).

The third instar larva of *P. flavipes* differs significantly in general appearance from those of other *Procecidochares* species studied to date (Green et al. 1993, unpublished data). *Procecidochares flavipes* is elongate and ellipsoidal and covered on most of its anterior end with many small, papillate, rugose pads; whereas *P. stonei* and *P. minuta* are barrel-shaped and have much fewer and larger rugose pads confined to the gnathocephalon (Green et al. 1993). The shape of the gnathocephalon in *P. flavipes* is more similar to other flowerhead-infesting tephritids than to its gall-forming congeners (Headrick and Goeden 1990a, 1991, Goeden and Headrick 1991a, 1992, Green et al. 1993). For example, in larval specimens separately identified as *P. minuta* from adults reared from flower heads of *Chrysopsis villosa* (Pursh) Nuttall and from galls on *Chrysothamnus nauseosus* (Pallen) Britton the gnathocephalon is subovoid, but broader than long and dorsally flattened (unpublished data). The gnathocephalon in *P. stonei* is flattened dorsally and rounded latero-ventrally (Green et al. 1993).

Although *P. flavipes* differs in general appearance from other *Procecidochares* species studied to date by SEM (Green et al. 1993, unpublished data), the type of sensory structures and their placement is consistent in all three of those *Procecidochares* species,

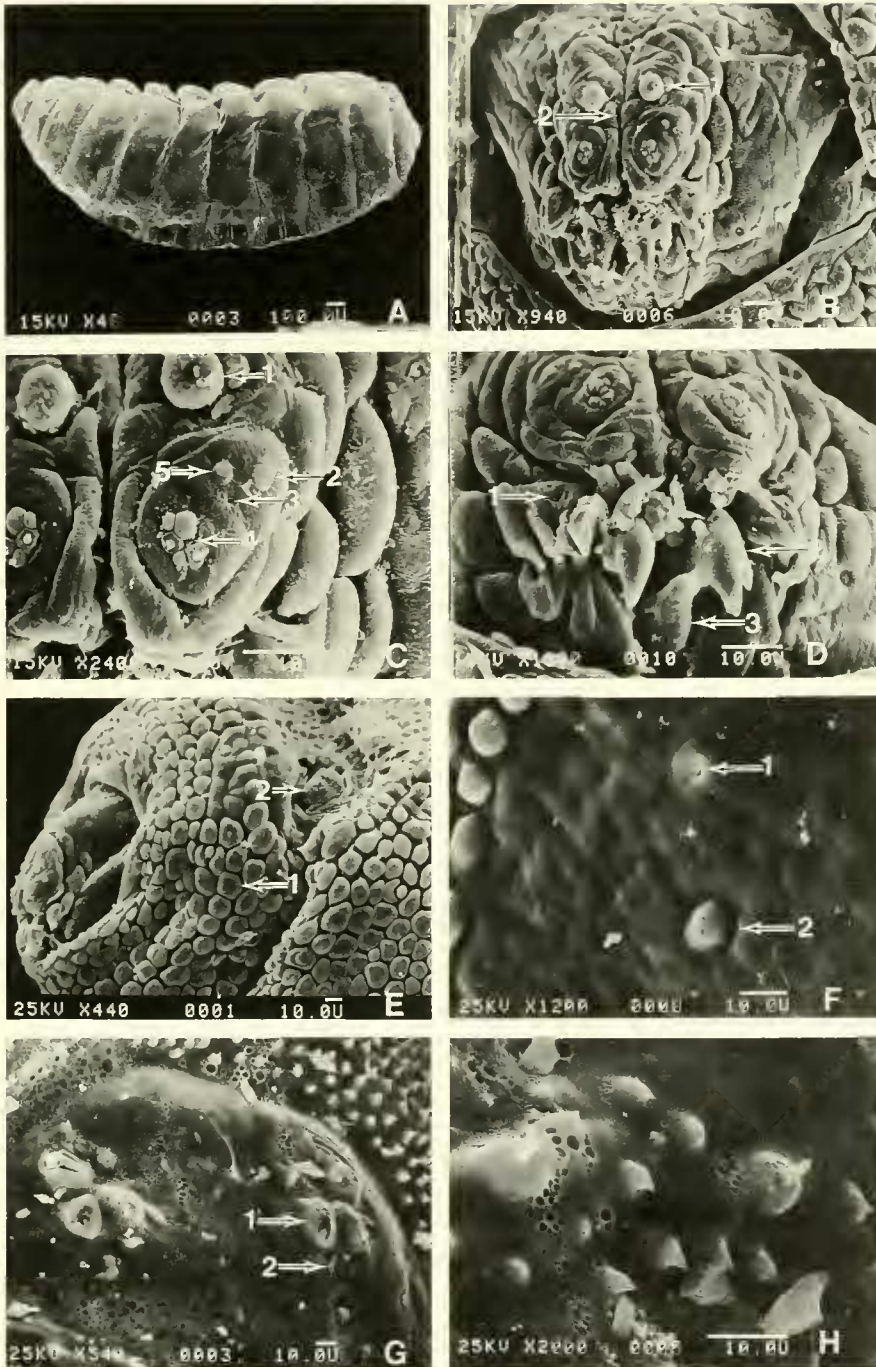


Fig. 2. Third instar larva of *P. flavipes*. (A) Habitus, anterior to left. (B) Gnathocephalon, anterior view. 1—dorsal sensory organs; 2—medial depression. (C) Gnathocephalon, anterior view. 1—dorsal sensory organs; 2—lateral sensory organ; 3—pit sensory organ; 4—terminal sensory organ; 5—unnamed sensillum. (D) Gnathocephalon, anteroventral view. 1—stomal sense organs; 2—mouth hooks; 3—median oral lobe. (E) Cephalic end, left lateral view. 1—rugose pads; 2—anterior thoracic spiracles. (F) Lateral sensory complex. 1—spiracle; 2—sensillum. (G) Caudal segment. 1—rima; 2—interspiracular process. (H) Caudal segment, stелеx sensilla.

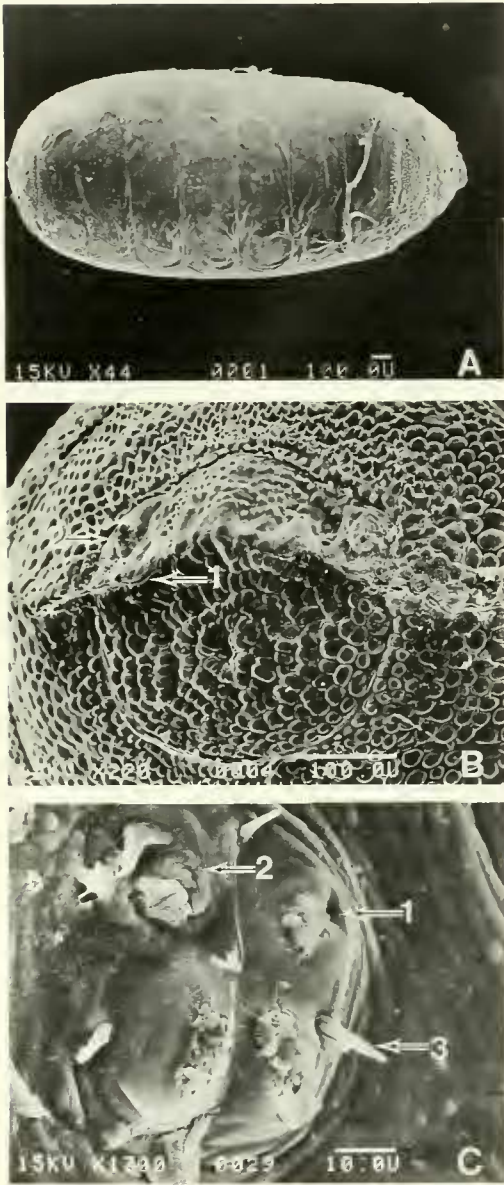


Fig. 3. Puparium. (A) Habitus, anterior to right. (B) Cephalic end, anterior view. 1—invagination scar; 2—anterior thoracic spiracles. (C) Caudal end, detail of posterior spiracular plate. 1—rima; 2—ecdysial scar; 3—interspiracular process.

including *P. flavipes*. The median oral lobe is lanceolate and basally free of the labial lobe in all *Procecidochares* species, including *P. flavipes*, examined by us (Green et al. 1993). All three *Procecidochares* species

studied also have similarly shaped anterior spiracles with two to three papillae. The lateral spiracular complex consists of an open spiracle with just a single verruciform sensillum for each *Procecidochares* species. The posterior spiracular plates also are similar among species of *Procecidochares* examined, though reduced slightly in *P. minuta* and *P. stonei* (Green et al. 1993, unpublished data).

**Puparium.**—Puparium black, elongate ellipsoidal, rounded anteriorly (Fig. 3A); anterior end, thoracic segments rugose; acanthae on dorsum of thoracic segments; anterior end bears invagination scar (Fig. 3B-1), raised anterior thoracic spiracles, dorsolaterad of invagination (Fig. 3B-2); posterior spiracular plates bear slightly raised, oval rimae (Fig. 3C-1), ecdysial scar (Fig. 3C-2), and four, thorn-like interspiracular processes (Fig. 3C-3) measuring ca. 0.01 mm long.

The puparium of *Procecidochares flavipes* differs significantly in appearance from *P. stonei* and *P. minuta*. The latter two species are superficially smooth, with no rugose pads or acanthae. The posterior spiracular plates in *P. minuta* and *P. stonei* are greatly reduced with the interspiracular processes barely distinguishable (Green et al. 1993, unpublished data).

DISTRIBUTION AND HOSTS

Foote and Blanc (1963) and Foote et al. (1993) mapped collection records for *P. flavipes* from California and from North America north of Mexico, respectively. Its geographic distribution was described by Foote and Blanc (1963) as “California; also islands west of Mexico,” the former state represented by only a single location in Riverside County in southern California. We add the following new rearing and location records from mature flower heads from California acquired by RDG since 1980: *Brickellia arguta* Robinson, 19 ♂ and 8 ♀, W side of Tecopa Pass at 1260-m elevation, Kingston Mountain Range, Inyo Co., 29.v.1991;

*B. californica*, 10 ♂ and 5 ♀, Kitchen Creek, Cleveland National Forest, San Diego Co., 16.ix.1981; plus the following rearing records (in chronological order) from this host in other counties: 9 ♂ and 18 ♀, Greenhorn Mountains, Sequoia National Forest (northern section), Kern Co., 8.ix.1982; 3 ♂, N side Westgard Pass, NE Inyo Co., 15.ix.1982; 1 ♂ and 1 ♀, NW of Kessler Peak at S end of Ivanpah Mountains, NE San Bernardino Co., 21.x.1982; 2 ♂ and 3 ♀, Quatal Canyon, Inyo National Forest, S Kern Co., 31.viii.1983; 5 ♂ and 1 ♀, Westgard Pass, Inyo National Forest, Tulare Co., 9.x.1986; 64 ♂ and 55 ♀, Santa Rosa Mountain truck trail, San Bernardino National Forest, Riverside Co., 4.x.1988; *B. desertorum* Coville, 14 ♂ and 4 ♀, S of Mountain Pass, NE San Bernardino Co., 20.ix.1983; plus the following record from this host in another county: 2 ♂ and 2 ♀, S of Potrero and N of Tecate, Mexico, at 620 m, S San Diego Co., 20.x.1987; *B. oblongifolia*, 13 ♂ and 12 ♀, Santa Rosa Mountain truck trail at 1400 m, San Bernardino National Forest, Riverside Co., 3.vi.1987. A male-biased sex ratio is suggested by these rearing data, as reported for *Procecidochares* sp. by Silverman and Goeden (1980).

This oligophagous tephritid appears to be restricted to the flower heads of only certain species of *Brickellia* in the Tribe Eupatorieae of the Asteraceae (Foote et al. 1993). The flower heads of five other species of *Brickellia* sampled by RDG to date have yielded either only *Trupanea* (Goeden 1985, 1992), *Paroxyna*, or no Tephritidae (RDG, unpublished data).

#### BIOLOGY

**Egg.**—The egg is inserted pedicel-last, loosely, and singly among the small, unopen, central florets in a pre-blossom flower head (Fig. 4A). Of 145 infested, mature flower heads of *B. californica* examined, only 12 contained two individuals, the rest held one *P. flavipes* puparium each. Two of 19 infested heads of the very closely related *B.*

*desertorum* contained two individuals. One of 10, individually caged, larger heads of *B. oblongifolia* yielded three adults and one parasitoid of *P. flavipes*, and upon dissection was found to contain four empty puparia; the other nine heads yielded either one or two flies, and upon dissection were found to contain no more than two puparia of *P. flavipes*. However, some heads of *B. oblongifolia* that yielded one *P. flavipes* adult also produced one or more adults of the five species of *Trupanea* reported from this same host by Goeden (1985, 1992), or upon dissection also were found to contain one or more puparia of *Trupanea* (Goeden 1992) or an unidentified species of Cecidomyiidae. Therefore, females of *P. flavipes* apparently usually oviposit one, occasionally two, but only rarely more than two eggs in individual, immature flower heads. The four puparia of *P. flavipes* in the single head of *B. oblongifolia* also may have been the progeny of more than one female.

**Larva.**—The newly hatched first instar immediately begins feeding on the inner side and soft interior of an immature ovule (Fig. 4B). It initially confines its feeding to this single ovule and scrapes away a crescentic, open excavation, but leaves intact its opposite, outer surface. As the larva grows and molts, it attacks additional adjacent achenes and enlarges its moist, open, smooth surfaced, centrally located feeding cavity, but usually still confines its feeding to the achene layer (Fig. 4C). Fully grown, third instars slightly scored the receptacles in only six (4%) of the 145 infested heads of *B. californica* examined. Most feeding chambers were formed well above the receptacle, but were connected to this nutritive tissue by the caruncula-bearing, basal, uneaten seed coats of the achenes, the uneaten fragments of which form the outer walls of these chambers. This caruncula-connection continued to conduct sap to the inner, scarified surface of the feeding chamber, and thus helped to supplement the diet of the developing larva. Thus, the larvae of *P. flavipes* fed, devel-



Fig. 4. Life stages of *P. flavipes* on *Brickellia* spp.: (A) two eggs inserted among ovules in immature flower head of *B. oblongifolia*, (B) first instar feeding in ovule of *B. californica*, (C) third instar feeding on soft achenes in head of *B. californica*, (D) puparium among scored achenes of *B. californica*, (E) resting female, dorsal view, (F) mating pair, ventral view.

oped, and grew within a bundle of concurrently growing and elongating achenes, which externally appeared intact and were full-sized at pupariation (Fig. 4C). An average of  $9 \pm 0.1$  (range, 4–12) achenes were scored and thus involved in the construction of the 145 cells examined in heads of *B. californica*; an average of  $8 \pm 0.6$  (range, 5–12) achenes in the 19 infested heads of *B. desertorum*; and an average of  $7 \pm 0.5$  (range,

5–12) achenes in 10 heads of *B. oblongifolia* solely infested by *P. flavipes*. There was absolutely no sign of gall-formation by *P. flavipes*! This finding is contrary for what otherwise has been regarded as a "large (with 10 species or more)," "typical," cecidogenous genus of nonfrugivorous Tephritidae (Freidberg 1984). Freidberg (1984) noted that all 12 species of *Procecidochares* with known modes of development are gall for-

mers. Instead, we document herein seed-feeding, non-gallicolous, larval development by this tephritid in a genus otherwise thought to be comprised of obligate, gall-forming species. This relationship appears to be the converse of facultative or obligate gall-formation among species of *Tephritis* (Goeden 1988, 1993) and *Trupanea* (Goeden 1985, 1987, 1992), most of which develop in flower heads without producing galls (Freidberg 1984).

**Puparium.**—Prior to pupariation, the third instar ceases feeding and orients itself lengthwise within the narrow flower head with its anterior end directed away from the receptacle (Fig. 4D). Pupariation occurs within the feeding chamber, 26 of which in heads of *B. californica* averaged  $2.6 \pm 0.3$  (range, 1.7–3.4) mm in length and  $1.1 \pm 0.1$  (range, 0.8–1.3) mm in width, and which thus closely approximated the size of the puparium. The puparium is lightly glued to the sides and base of the chamber by a mixture of dried sap and liquid feces, as are the scored achenes that comprise each chamber. The two puparia contained in a few single heads of the small-headed *B. californica* and *B. desertorum* were each formed in separate chambers that only slightly coalesced laterally in the common achene wall fragment that separated them. In the single, larger head of *B. oblongifolia* found to contain four puparia of *P. flavipes*, three were formed touching at staggered levels within a common, central chamber formed within 10 achenes; whereas, the other puparium occupied a separate cell displaced to one side of this head.

**Adult.**—Adults (Fig. 4E) exit the heads via a 3–6 mm channel through the pappus hairs of *B. californica*. Males and females emerged concurrently from one bulk, flower-head sample during a 2-week period in the insectary. Females are synovigenic, and contain neither substantial fat body tissue nor mature or nearly mature ovaries at emergence, unlike *Procecidochares* sp. on *A. dumosa* (Silverman and Goeden 1980) and

*P. stonei* on *Viguiera* spp. (Green et al. 1993) in southern California. However, these reproductively immature adults of *P. flavipes* readily mated in laboratory arenas (Fig. 4F).

The abdominal cavity of newly emerged adults is nearly entirely filled by the crop. We “rediscovered” the crop while dissecting *P. flavipes* adults for examination of their reproductive organs. The crop walls are thin and so closely associated with the walls of the abdominal cavity that the crop is easily penetrated during dissections, often unknowingly. During one dissection, the crop peeled away from the abdominal walls intact and we found it to be a large, striated, blind sac containing clear fluid (Fig. 5A, B). The crop originates as a ventral opening of the foregut opposite the proventriculus (Fig. 5A). A small tube, termed a “crop duct,” travels along the ventral aspect of the midgut and expands into the crop proper as it enters the abdomen. The walls of the crop duct and crop are bilaminar with an inner cuticular layer and an outer muscular layer. The walls of the fluid-filled crop are pressed against the interior of the abdominal cavity and displace the remaining midgut, hindgut and reproductive organs against the dorsal aspect of the abdominal cavity (Fig. 5B). Thus, the abdomen is virtually filled by the crop until the reproductive organs begin to mature, when they in turn displace the crop as they enlarge. Dean (1934) described and illustrated a similar crop in the apple maggot, *Rhagoletis pomonella* Walsh. In preliminary experiments, *P. flavipes* adults were allowed to feed freely from food and water sources from which they were later deprived to determine the rate of crop content usage. Adults depleted their fluid stores over the course of ca. 3 days to the point of abdominal collapse. Thus, the shape of the abdomen depends on the amount of fluid stored in the crop. When later allowed access to food and water adults imbibed fluids until their crops were filled. The process of filling the crop lasted ca. 2 min. Droplet formation, or crop welling (Adams and Heath



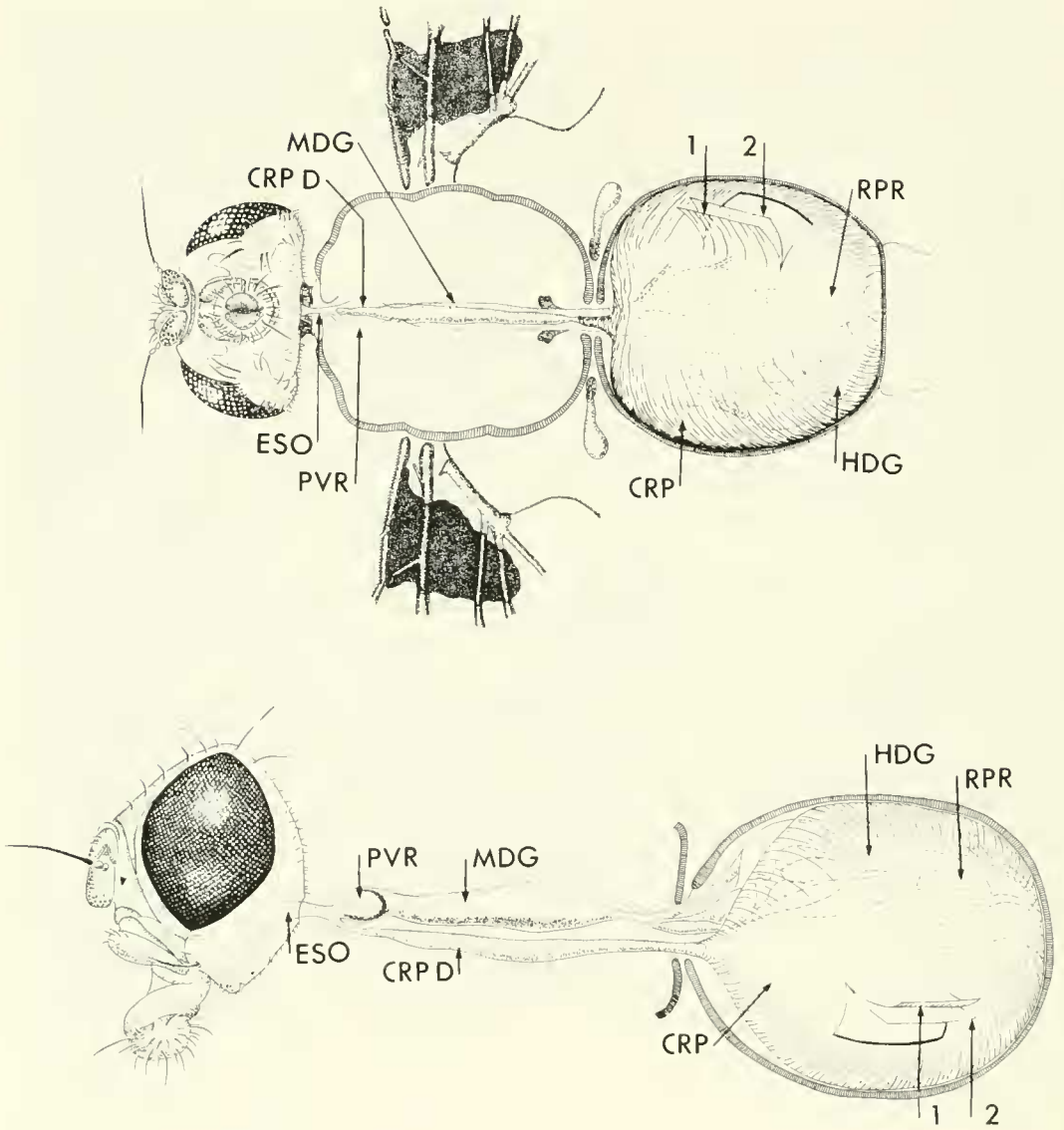


Fig. 5. The crop. (A) Adult: frontal section, ventral view. (B) Adult: parasagittal section, left lateral view. CRP—crop, 1—outer muscular layer, 2—inner cuticular layer; CRP D—crop duct; ESO—esophagus; HDG—hindgut; MDG—midgut; PVR—proventriculus; RPR—reproductive organs.

1964), then followed and the first waste was produced after ca. 30 min. The large size and unusual anatomy of the tephritid crop stimulated further study of several other tephritid species, which will be reported separately. The adaptive nature of the crop in

*P. flavipes* is discussed below under “Seasonal History.”  
*Wing displays:* Rapid enantion, as described by Green et al. (1993) for *P. stonei*, was displayed by both sexes of *P. flavipes* in arenas, both spontaneously and directed

towards individuals of the opposite sex. Females also displayed a slower enantion that was followed by hamation (Goeden and Headrick 1992), during which the wings were extended to 60° from the longitudinal body axis, then hamated through ca. 30°, i.e. one wing was extended to 90° while the other wing was brought back to 60°.

*Courtship:* Courtship behaviors other than the wing displays described above were not observed with *P. flavipes* in laboratory arenas, and reproductive behavior was not observed in the field. In arenas, males stalked females or jumped on them from behind opportunistically as they walked past, with or without accompanying wing displays. The intensity of these wing displays increased as the male neared the female. Females either did not respond with wing displays to males and remained still, or decamped. If the female did not move, the male ceased his wing displays, then attempted to mount her by jumping onto her dorsum. Males attempted to mount females from as far away as 5 cm in arenas. Most mounting attempts were unsuccessful, with the males missing the females or failing to hold onto them after mounting. Females of *P. flavipes* used their legs and wings to strike at males after being mounted, but then became quiescent once the male obtained a firm grasp.

*Copulatory induction behavior:* Once a male successfully grasped a female, he positioned himself for copulatory induction behavior (CIB). During CIB, which typically was of short duration, the male grasped the female with his front legs around her abdomen near her thorax, his middle legs near the base of her oviscape, and his hind legs bent underneath her oviscape and abdomen. His hind legs were used to pull the ovipositor apex to the epandrium and to drum asynchronously on the oviscape and posterior sternites of the abdomen. Typically, the female exerted her aculeus within seconds after a male began CIB; however, in one pairing, a male remained mounted on a female for 30 min before she exerted

her aculeus. Female resistance to copulation was not observed, as a female exerted the aculeus for any male able to maintain a grip after mounting her.

*Copulation:* The aculeus was lifted by the male to expose the gonopore between it and the 8th sternite. The aedeagus was visible on video-recordings exiting posteriorly from between the surstyli and the epandrium, coiling around the right side, and entering the gonopore. In the final copulatory position, the male had his front legs on the anterior of the abdominal tergum of the female, bent at the femoro-tibial joint and level with his mouthparts. The fore femora were parallel to the long axis of the body of the female. The middle legs of the mounted male were placed near the base of the oviscape, and his hind legs were held underneath or pressed against the sides of the oviscape. The wings of the female were spread at 45° from the longitudinal body axis; the wings of the male were held flat over his dorsum with their costal margins parallel. Females *in copula* responded to moving objects by facing toward the source and displaying a single wing enantion without supination, i.e. by extending their wings from their resting position through an arc of 20°.

The aculeus was intermittently exerted during copulation by the female, an action which pushed the male posteriad and extended his postabdomen by means of membrane expansion. When the female exerted her aculeus, the male responded with vigorous CIB, i.e. the apex of his hind tibia and hind basitarsus were rubbed synchronously, posterior to anterior, along the sides of her oviscape. Each leg rubbed the oviscape three to five times per second, then rested. During full exertion of the aculeus by the female, the male was nearly pushed off her dorsum as he held onto her aculeus with his hind tarsi; thus, no CIB was exhibited, as he had to maintain his grip until the female retracted her aculeus.

Twenty-three of a total of 38 copulations

were observed from their inception. Copulations averaged 5 (range, 2–9) h in duration. Pairs copulated up to twice daily ( $n = 8$ ) from morning to night, and all pairs in all trials mated more than once. Copulation occurred in laboratory arenas during the late fall in 1990, and with  $F_1$  flies during the early summer in 1991.

*Aggression:* In arenas, females occasionally displayed aggression expressed as rapid wing enantion and lunging at males. In one such response, a female turned to face the stimulus and extended her wings synchronously while vibrating them rapidly in a plane parallel with the blade. She then extended both wings to  $90^\circ$  from the midline of her body while she also supinated them  $90^\circ$ , and then returned them immediately to their resting position flat and partly overlapping upon her dorsum. This behavior was similar to the aggression/defensive displays by females of *Neaspilota* (Goeden and Headrick 1992, unpublished data). The female backed away while continuing to face the stimulus, and repeated her enantion display until she turned away and groomed.

*Longevity:* Adults are long lived; 20 virgin females caged separately lived an average of  $103 \pm 6$  (range, 61–162) days in the laboratory. Under insectary conditions, another series of 11 females lived  $42 \pm 5$  (range 22–78) days; whereas, eight males lived  $39 \pm 12$  (range, 21–54) days.

*Seasonal history.*—*Procecidochares flavipes* is multivoltine, like several other oligophagous, nongallicolous Tephritidae in southern California, e.g. *Neaspilota viridescens* Quisenberry (Goeden and Headrick 1992), *Neotephritis finalis* (Loew) (Goeden et al. 1987), *Trupanea bisetosa* (Coquillett) (Cavender and Goeden 1982), *T. californica* Malloch (Headrick and Goeden 1991), and *Paracantha gentilis* Hering (Headrick and Goeden 1990b). It reproduces in a succession of spring-blooming (*Brickellia arguta* and *B. oblongifolia*) and fall-blooming Asteraceae (*B. californicum* and *B. desertorum*), along with several species of *Trupa-*

*nea* (Goeden 1985, 1992). Both the summer and winter are passed as sexually immature, long-lived adults, probably in riparian habitats, i.e. canyons and washes on desert margins, mountain meadows, and stream margins, waiting for a resumption of flowering by its alternate hosts, again, in the manner of other native, nongallicolous Tephritidae in California (Cavender and Goeden 1982, Goeden et al. 1987, Headrick and Goeden 1990b, 1991, Goeden and Headrick 1992). There are at least two generations each year, an  $F_1$  produced in spring and  $F_2$  in the fall on the alternate hosts identified above, and possibly an additional generation in late spring, summer, or early fall on these or other species of *Brickellia* as yet undetected.

We hypothesize that the crop is adapted as a water storage organ in *P. flavipes* and other tephritids that exhibit similar, long-lived, life cycles in California, e.g. *Trupanea conjuncta* (Goeden 1987), *Paracantha gentilis* (Headrick and Goeden 1990b). Long periods without rainfall are characteristic of southern California's climate. By using the crop as a water-storage organ, *P. flavipes* adults may drink when opportunity allows as they overwinter or oversummer until their host plants are again in a stage suitable for oviposition. Because adults copulated readily after emergence in laboratory cagings, we assume that field populations also are capable of the same. Thus, overwintered or oversummered females begin oviposition after the maturation of their reproductive organs, which we suggest is tied to the phenology of their host plants. A following report will discuss the evolution and adaptation of the crop in the Tephritidae (Headrick and Goeden, unpublished data).

*Natural enemies.*—Three species of chalcidoid Hymenoptera were identified as parasitoids of *P. flavipes*. A solitary, primary, larval-pupal parasitoid, *Eurytoma* sp. (Eurytomidae), was reared from puparia of both *P. flavipes* and *Trupanea* spp. from heads of *B. oblongifolia*, where it was the principal parasitoid. *Eurytoma* sp. was not recovered

from *P. flavipes* in heads of *B. californica*, where, instead, *Pteromalus* sp. (Pteromalidae) was its principal primary, solitary, parasitoid reared from larva and puparia. The third parasitoid was *Colotrechnus ignotus* Burks (Eupelmidae) a few of which were reared as solitary, primary, ectoparasitoids of the young larvae of *P. flavipes* and *Trupanea* spp. in heads of *B. oblongifolia*.

#### CONCLUSION

The lack of gall formation by *P. flavipes*, its distinctive host preferences for *Brickellia* spp., the substantial morphological differences that distinguish its eggs, larvae, and puparia from those of the two other species of *Procecidochares* studied to a comparable degree in California (Silverman and Goeden 1980, Green et al. 1993), the posterior orbital bristles (reduced but present) and bicolored pterostigma of the adults noted as unique for North American *Procecidochares* by Foote et al. (1993), and our unpublished research on other species of *Procecidochares* all strongly suggest that this species is unique among North American species of *Procecidochares*, and may at some future date warrant its removal to a separate genus.

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